THE UPWARD TRANSLOCATION OF FOODS IN WOODY PLANTS. II. IS THERE NORMALLY AN UPWARD TRANSFER OF STORAGE FOODS FROM THE ROOTS OR TRUNK TO THE GROWING SHOOTS?

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There is apparently a very common belief that in most trees considerable quantities of the carbohydrates, that have been stored in the lower trunk and in the roots, move up as growth starts in the spring and are used in shoot and leaf formation.

The arguments which seem most commonly to be put forward as proof of such an upward transfer are that quantities of food are stored in the xylem tissues; that these are present in soluble form in the water-conducting vessels at the time spring growth commences; and that these foods rapidly disappear at about the time of this rapid shoot development. From these facts it would seem reasonable to think that the food had moved up with the water to the growing shoots, but, as shown in a recent paper (Curtis, 1920), the mere presence of soluble foods in water-conducting tissues cannot be considered as proof that the foods move with the water. In fact, it was shown that there is no appreciable longitudinal transfer of soluble foods through the xylem.

Some ringing experiments of Hartig's (1858) have also been considered as proof of the movement of foods from the roots to the growing shoots. At intervals of eight days from the first of April, 1857, until the middle of September of the same year, he ringed young oak trees of about the diameter of one's arm. The rings were two inches broad and were situated four feet from the ground. Some trees were also cut down at the time of ringing, but he does not state whether these were cut early or late in the season. Observations made in the spring of 1858 showed that all trees ringed previous to June 30, 1857, had lost the starch from below the rings, while those ringed after June 30 contained starch. The starch from these also, however, had disappeared by the fall of 1858. As the starch had not disappeared from some of the roots of the felled trees, he concluded that the food stored in the roots normally moves up with the water through the xylem and is used in shoot growth.

As has been previously shown, no appreciable quantities of food move longitudinally through the xylem and it seems very probable that the food below the rings disappeared because it was used in root growth and in diameter growth of the trunk. The only point tending to contradict this is that in some of the felled trees the starch did not disappear. This lack of

removal from the stumps of felled trees, however, may have been due to an excess of water following removal of the transpiring surface and resulting in a check on respiration or in death. When the stumps were healthy, as indicated by the development of shoots, the starch did disappear. Hartig failed to state the time at which trees were felled as well as the relative number of stumps which retained or lost their food stores.

The fact that the diameter growth of a trunk was very much decreased below a ring is additional proof that there is no large excess of food stored in the roots. Hartig explained this weak growth below a ring as due to the inability of the food, which he considered as moving up through the xylem, to move radially to the cambium. He believed that only that food coming through the phloem could be used in cambial growth.

Other data which have been considered as proof of the use of food from the roots for spring shoot growth have been presented by Leclerc du Sablon (1906) who determined the effects of ringing at different seasons on the amounts of carbohydrates found in roots and stems of a number of woody plants. He concluded that, as a general rule to which there may be exceptions, the roots of woody plants act as storage organs from which the carbohydrates move up in the spring. The data he offered, however, are far from conclusive. Some results he obtained in ringing experiments on the pear are presented in table 1.

The analyses for April 13 alone suggest that upward translocation from the roots might have taken place in the spring and that the ring has prevented this upward transfer, for in that tree ringed February 9 the roots

TABLE 1. *Data from Leclerc du Sablon to show effect of ringing on distribution of food between roots and stems of pear trees. Total carbohydrates expressed as percentage of dry weight.*

Date at which Sample Taken	Not Ringed		Ringed Feb. 9		Ringed May 8	
	Roots	Stems	Roots	Stems	Roots	Stems
Feb. 18	30.3	23.0	—	—	—	—
Apr. 13	22.4	21.3	25.6	18.3	—	—
June 16	27.9	23.7	27.9	29.5	17.5	29.0
Aug. 4	29.2	24.7	26.5	33.2	18.3	27.0
Sept. 24	33.8	25.7	19.3	29.1	21.4	29.5
Dec. 1	29.3	25.4	17.4	25.9	17.5	25.8

have a higher content than the check and the stems a lower content. But in a preliminary series (in 1904) he found similar differences between individuals taken at one time. For the quince, samples taken from four different plants on March 17 showed a maximum difference in carbohydrate content per 100 grams of dry material of 5.7 grams for roots and 4.9 grams for stems. With the pear, the corresponding differences were respectively 2.7 and 1.4. It is true that trees differing in external characteristics were definitely chosen for these samples, but similar differences might easily

have occurred between the other trees. Furthermore, the increases in carbohydrate content of the roots of ringed plants over that content found earlier in the season, shown on June 16 for those ringed on February 9 and as shown on June 16 and August 4 for those ringed May 8, would be hard to explain except as resulting from individual variations or from the healing of the wounds. In the quince, an analysis on April 13 showed greater carbohydrate content in the roots of the ringed tree than in those of the tree not ringed, but the stem of the ringed tree also showed a carbohydrate content greater than the stem of the check. Evidently the whole tree had a higher carbohydrate content.

Hartig, Leclerc du Sablon, Butler (1917), and others have shown that before growth starts in the spring the roots may contain a higher percentage of carbohydrates than the stems, but the stems have more supporting tissue and the percentage composition may therefore mean nothing unless the total mass is known. The actual amount of carbohydrates in the roots may be less than that in the tops, even though the percentage composition is high.

Data showing that the mass of carbohydrates stored in the roots is actually much less than that stored in the tops have been presented by Chandler (1917) who has calculated, from percentage concentrations obtained by Butler, the relative amounts of food available in the roots and tops of an apple tree. His data are presented in table 2.

TABLE 2. *Approximate amounts of dry matter, starch, and saccharose at the time buds are swelling, in case of a seven-year-old Bismarck apple tree that has been growing in sod.*

Part of Tree	Actual Dry Weights, Pounds	Pounds of Starch Calculated	Pounds of Saccharose Calculated
1-yr. twigs	3.15	0.98	0.12
Older branches	21.00	6.72	0.17
Trunk	15.13	5.14	0.11
Totals for parts above ground	39.28	12.84	0.40
Large roots	14.15	5.43	0.28
Small roots	6.49	2.37	0.06
Totals for roots	20.64	7.80	0.34

These figures are, of course, only suggestive, as the trees analyzed and the one weighed were grown under different conditions. But the error would tend to be in favor of large root storage, for the tree weighed had been grown in sod under conditions favorable to larger root growth. In this instance the roots weighed 52.5 percent as much as the tops. Pickering (1917) gives data showing the relative weights of tops and roots of a number of trees varying from 10 to 20 years old. The average root weight of 461 apple trees was 22.9 percent of the tops, that of 15 pears was 23.5 percent, that of 6 Damsons was 25.2 percent and that of 44 plums was 28.3 percent.

The relative root and top weights would, of course, vary with the soil and the climate, but there seem to be good indications that tree roots may not greatly exceed 50 percent of the top weight. Therefore, though the roots may have a carbohydrate content greater than the tops when measured as percentage of dry weight, the total quantity of carbohydrates in the roots is much less than that in the tops, and, since the roots must need quantities of food for their own use, it seems doubtful whether any is normally carried to the tops for shoot growth. The indications that root growth commences in the spring before shoot growth, as discussed later in this paper, may be considered as further proof that the food stored in the roots is used primarily by the roots.

Data obtained from experiments designed to determine the path of upward translocation, a subject reported in a recent paper by the writer (Curtis, 1920), offer evidence that little or none of the food stored in the trunks or roots of trees is normally moved up to be used by the developing shoots and leaves.

In one group of experiments, large numbers of twigs and branches were ringed early in the spring while the buds were still dormant or were just beginning growth. These rings were made at different distances from the tip in order to determine from how far back food was withdrawn for shoot growth.

Since, as was shown in the previous paper, no appreciable upward movement of foods occurs through the xylem, the growth of a shoot above a ring would serve as an approximate measure of the amount of food available. If the ring were back far enough from the growing tip to allow for growth practically as great as that on unringed twigs, it would seem that these twigs need not draw on the food stored at greater distances.

A large number of stems of *Acer saccharum* were ringed on April 5 at different distances from the tips. In one series the rings were in the first-year wood, in another in the second- or third-year wood, and in another the rings were in that part of the stem ranging from five to fifteen years old. Some of the stems had made terminal growths in the previous year of from only 1 to 10 centimeters, while others had made growths of from 20 to 40 centimeters. In each case a check stem was chosen as nearly matching the ringed one as possible. The check and ringed stems were usually the two terminals of a pair produced by dichotomous branching. Such a variety of branches was used that no attempt will be made to give more than a brief summary of the results.

Of 15 twigs ringed in the one-year-old wood, the average terminal growth on May 6 was 0.84 cm. That of the corresponding stems not ringed was 2.22 cm. Of those ringed in the two- and three-year-old wood the average terminal growth was 2.03 cm., while that of the corresponding checks was 2.25 cm. The leaves of the ringed stems in these cases did not show the bronze tinges that were common in the normal young leaves, but

were a bright green. At the same date, May 6, there were no apparent differences in the growths of stems not ringed and of those ringed back on the 5- to 15-year-old stems. On May 25 measurements were made of these stems. An average of the shoots of ten stems of this series showed a growth of 9.96 cm., while that of the corresponding check stems was 11.09 cm. The older stems, whether the diameter was large or small, showed growth fully as great as that of those not ringed, but some of the younger stems showed somewhat lessened growth which lowered the average for the growth of ringed stems. In most cases growth had ceased and terminal buds were beginning to develop at the time of measuring.

On April 7, a number of stems of a pear tree growing in sod were ringed. These stems ringed in the one- and two-year-old wood showed distinctly lessened shoot growth, but those ringed where the diameter was from 1.5 to 3 cm. showed growth fully as great as that of the unringed stems.

On May 16, 1919, stems of an apple tree that was just beginning growth were ringed just below the base of the one-, two-, and five-year-old wood. At the time of ringing, the lengths of the shoots measured to the tips of the infolded leaves were from 1.5 to 2.0 centimeters. At the same time a single branch was ringed at its base where it measured 3.8 centimeters in diameter. The diameter of the main trunk just below the lower limbs was 11.0 centimeters. All the stems ringed in the fifth-year wood (group 4) were less than one centimeter in diameter at this point, with the exception of those lettered *c* and *j* which were respectively 1.2 and 1.5 centimeters in diameter. The growth was completed in most of the twigs when the measurements were taken on June 15. These data are recorded in table 3.

TABLE 3. *Pyrus malus. Ringed May 16, 1919. Measurements taken June 16. All of the same letter excepting in column 5 were closely matched. Column 5 and letters a to h on one tree, i to n on another. The data are represented as growth in centimeters.*

	1 Not Ringed	2 Ringed Below Base of One-year-old Wood	3 Ringed Below Base of Two-year-old Wood	4 Ringed Below Base of Five-year-old Wood	5 Ringed at Base of Branch 3–8 Cm. in Diameter
a.....	17.5	1.0	4.5	11.5	12.5
b.....	14.5	0.7	.5	5.0	13.0
c.....	9.5	0.4	3.0	10.0	13.0
d.....	15.5	0.4	2.0	9.0	12.5
e.....	17.0	*3.0 wound healed	6.0	21.0	10.5
f.....	16.0	1.0	—	11.5	
g.....	10.5	*5.5 wound healed	3.5	10.5	
h.....	10.0	2.5	*1.5 broken	—	
i.....	14.5	*2.5 wound healed	6.5	10.0	
j.....	19.5	0.4	4.5	13.5	
k.....	17.5	1.5	6.0	—	
l.....	18.5	1.8	7.0	—	
m....	17.0	*6.5 wound healed	3.5	—	
n.....	14.5	*3.0 wound healed	4.0	9.5	
Ave.	15.14	1.08	4.42	11.15	12.3

* Not included in average.

From the table it seems that shoot growth is fairly vigorous when no food further back than that obtained from a branch about one centimeter in diameter is available.

A somewhat similar experiment was tried with *Fagus grandifolia*. In this case the ringing was done before the buds had started. The data are reported in table 4.

TABLE 4. *Fagus grandifolia. April 7 to May 24.*

	Ave. Length of Shoot in Mm.	Ave. Number of Leaves
Twigs not ringed	186.4	6.6
Ringed in the middle of the one-year-old wood	21.4	2.1
Ringed at the base of the one-year-old wood	42.8	3.3
Ringed in the wood three to five years old which in all cases was less than one centimeter in diameter	59.1	5.0

These data as well as those reported in a previous paper (Curtis, 1920, tables 8–10) indicate that, when the ring is no further back than the 5- to 10-year-old wood, the growth of the shoots above the ring approaches more and more nearly that of the unringed stems. It will be necessary to use larger numbers of branches before one can attempt to state the distance from which food may be withdrawn.

Even if one could use large numbers of uniform stems that have been grown under uniform conditions, it would be difficult to determine from ringing experiments alone as to the exact distance of upward movement, for a check in growth may result not from lack of food but from lack of water due to the fact that no new xylem would be formed in the region of the ring, because in some trees much of the water may be carried through this new xylem. It is to be noted that, in practically every case in which the wound was not well protected by a coating of paraffin, the growth was distinctly decreased as a result of a deficiency of water due to drying of the xylem.

Not only is there considerable food stored in the twigs and young branches which becomes available for shoot growth in the spring, but the food manufactured by the new leaves soon after they open also becomes available for continued shoot growth.

The data reported in table 5 indicate that, soon after the shoots have started, much or all of the food necessary for continuing growth is produced by the leaves of that same shoot.

In the experiments with apple and in the first of the experiments with Ligustrum, the growth of the ringed twigs with leaves is fully as great as that of the twigs not ringed. In fact, in these two cases the data indicate that ringing has even increased growth above that in the checks. This may be because the ring has increased the food supply by preventing removal of that produced by the new leaves. In the other experiments, with the exception of the 1918 experiment with Philadelphus, the growth of the ringed

stems which retain their leaves is nearly as great as that of the normal stems. Even the results of the 1918 experiment with Philadelphus are not in opposition to the hypothesis that a large part of the food used for continued growth of a stem is produced by the leaves of that stem, for, as indicated in table 5 and also in the more detailed tables 1 and 2 of the previous paper, only about one third of the current year's growth was above the ring in the 1918 experiment and this part carried only the younger leaves, while in the 1919 experiment the entire new shoot with all its leaves was above the ring. The fact that the stems which were defoliated for a distance of from 15 to 20 centimeters from the tips in 1918 (group 3) showed such good

TABLE 5. *Experiment to determine how much food used in shoot growth may be produced by the leaves of that shoot.*

	1 Not Ringed, Leaves Remaining		2 Ringed, Leaves Remaining		3 Not Ringed, Leaves Removed		4 Ringed, Leaves Removed	
	Original Length of Shoot	Gain in Cm.	Original Length Above Ring, Cm.	Gain in Cm.	Original Length of Part Defoliated	Gain in Cm.	Original Length Above Ring	Gain in Cm.
Apple. June 11 to June 30. Ave. of 6 stems	25.0	4.48	15.0	5.3	15.0	3.37	15.0	0.25
Ligustrum ovalifolium. June 18 to July 3. Ave. of 7 stems		13.61	21.7	14.61	22.0	7.41	21.7	0.71
Ligustrum ovalifolium. June 19 to July 3. Ave. of 6 stems		12.41	20.8	10.58	20.9	5.75	21.1	0.23
Ligustrum ovalifolium. July 6 to July 22. Ave. of 6 stems		12.23	11.8	7.2	10.9	7.62	11.8	0.28
Ligustrum ovalifolium. July 11 to July 22. Ave. of 25 stems		9.94	17.8	8.19				
Philadelphus pubescens. May 30 to June 8, 1918. Rings in new growth. Ave. of 5 stems	54.6	34.1	17.0	11.75	17.0	27.0	17.0	0.5
Philadelphus pubescens. May 30 to June 4, 1919. Rings in old wood below base of new growth Ave. of 14 stems	18.8	16.36	21.1	12.96	17.4	7.96	18.5	1.16
Philadelphus pubescens. June 3 to June 6, 1919. Rings in old wood below base of new growth. Ave. of 8 stems	37.6	9.38	38.4	7.13	40.0	3.56	30.8	1.44

growth, while the shoots of the 1919 experiment (group 3) showed such poor growth gives additional proof that the leaves of the new shoot supply a large part of the food used in growth after a few leaves have once opened. In 1918 that food was available which was produced by the many leaves on the lower non-defoliated part of the stem, while in 1919 only stored food was available as the entire new shoot was defoliated.

Discussion

The available data are not sufficiently extensive to enable one to conclude from how far back food is withdrawn to be used in shoot growth. It is probable that the amount of upward movement depends upon the kind of tree, its age, and conditions of previous growth, as well as on conditions during the current season.

Leclerc du Sablon suggested that some trees may store but little of their food in the roots, while others store quantities there to be used later in shoot growth, but his experiments supposedly proving the latter condition are far from convincing. It is to be noted that he used young trees only three to four years old, and, though his data offer no conclusive proof, it is possible that such young trees might show more upward transfer of foods; but it is just as possible that, when a tree becomes well established, there is normally very little upward translocation. Other conditions being equal, one would expect little or no withdrawal of carbohydrates from below if during the spring growing season there were a deficiency of water and perhaps of mineral nutrients, especially nitrates, and the days were bright. Under such conditions vegetative growth would tend to become checked early, and the new leaves would soon begin to accumulate carbohydrates through photosynthesis.

If root growth commenced in the spring before shoot growth, or even if growth began in both at about the same time, one would expect that most of the food present in the roots would be immediately needed by the roots. No very conclusive evidence on this point is available, but Goff (1898) found that root growth may commonly precede the swelling of buds. Observations were made by digging trenches early in the spring and measuring the amount of new growth that had occurred up to the time of digging. Such early root growth was found to occur in the following plants: *Acer saccharum*, *Pyrus malus*, *Pyrus communis*, *Prunus cerasus*, *Prunus virginiana*, *Betula alba*, *Morus alba*, *Cornus stolonifera*, *Eleagnus hortensis* var. *Songorica*, *Ribes rubrum*, *Ribes nigrum*, *Ribes oxyacanthoides;* as well as in nine species of gymnosperms and a few herbaceous perennials. There were only two possible exceptions recorded.

Furthermore, data presented by Jones (1903) would indicate that root growth precedes stem growth. It was found that the water content of the trunk of the sugar maple increased from 31.5 percent in December to 36.5 percent in March, while from March 15 to April 28 the water content increased to 47 per cent. After this date the buds opened and the water content fell off. This rapid increase in water content just previous to the opening of the buds, which occurs not only in the maple but in all the other deciduous trees examined, though it cannot be considered as conclusive proof, yet at least suggests that the absorbing organs, the roots, have started growth early, making possible a rapid absorption of water just previous to shoot growth.

The data obtained from ringing dormant stems show that, when the ring is no further back from the growing tip than that part of the branch from 5 to 15 years old or from one to five centimeters in diameter, the growth may be practically as extensive as when no ring is made. When the growth was somewhat lessened by ringing, it may have been due, not to a lack of food, but to a deficiency of water, as the ring, of course, prevented the formation of a new layer of xylem. Furthermore, although the rate of starch loss was more rapid when the ring was near the tip, indicating more complete usage of stored food, yet the rate of starch loss when the ring was in the older wood was approximately the same as from a normal stem. These results indicate that normally very little food is withdrawn and carried up from the main trunk or roots to be used in shoot growth. It would seem therefore that, especially in older trees, the food in the branches is more than sufficient to initiate shoot growth, and that, since much of the food necessary for continued growth may be produced by the young leaves, there may be no tendency to draw upon that food stored in the roots. Furthermore, the fact that a cutting no longer than six inches may produce a short shoot with leaves and also a callus and roots, when no food can be obtained from storage organs outside that small bit of stem, would indicate that a shoot on a large branch need not draw on food stored at great distances, as from the trunk or roots.

There seems to be little foundation for the statement (Butler, 1917) that the carbohydrate stored in the young root tip is digested in the spring and carried up the trunk to the stems for shoot formation. It seems more probable that the roots themselves use nearly all, if not quite all, of the foods stored in them. When one considers that root growth probably commences earlier in the spring than shoot growth and may also continue later in the fall; that at no time can roots produce their own foods, as can the shoots as soon as a few leaves form; and that the tree roots probably store a smaller mass of food than do the tops, it is then difficult to see how food from the roots can be of very great aid in the shoot formation of a tree.

Summary

Facts commonly considered as proving that the food which is stored in the roots and lower trunks of many trees is carried up to be used in shoot formation cannot be considered as actually proving such upward movement.

When a ring is made on that part of a stem from 5 to 15 or more years old or from one to four or more centimeters in diameter, the growth above the ring approximates that of a normal stem, which fact indicates that upward movement of food from points below the ring is not essential.

When shoot growth is well started, much of the food used for continued growth may be produced by the leaves of that shoot, which fact indicates that considerable growth may take place when but little stored food is available.

The data at hand are not adequate to settle the question as to how far back from the tip food is withdrawn to be used in shoot growth. In fact, the amount of removal probably varies with different species and with different individuals, depending on the conditions of the current as well as of previous seasons. It seems very probable, however, that there is normally no upward movement of foods from the roots and perhaps little or none from the main trunk.

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